

MONOECY AND SEX CHANGES IN *FREYCIKETIA* (PANDANACEAE)¹

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ABSTRACT

In cultivation, two species of the basically dioecious genus *Freycinetia* (Pandanaeae) have produced pistillate and staminate inflorescences both sequentially and simultaneously on individual plants. These findings are discussed, together with other cases of occasional deviations from dioecy.

According to most textbooks and general reference works the genus *Freycinetia* is considered to be dioecious (Warburg, 1900; Heywood, 1979; Dahlgren et al., 1985; Stone, 1984), although some exceptions have been noted (Stone, 1972; Cox, 1981; Cox et al., 1984), drawing attention to the significance of these presumably rare exceptions to the dioecious condition. In *Freycinetia reineckeii* Warb., Cox has observed functionally bisexual spikes, and both pistillate and staminate inflorescences on the same branch in *Freycinetia scandens* Gaudich., and Stone (1972) has noted the same in *Freycinetia negrosensis* Merr. and *F. imbricata* Blume.

The following observations made in the tropical greenhouses of the Hamburg Botanical Garden confirm and extend these earlier observations and, by adding some new pieces to the puzzle, seem to indicate that sex expression in this genus is to a considerable extent under environmental control. Both *Freycinetia funicularis* (Savigny in Lam.) Merr. and *F. cumingiana* Gaudich. (synonymous with *F. luzonensis* Presl, according to Stone) have been observed to show monoecy.

Both of the species mentioned above are easily cultivated from cuttings, and the material in cultivation probably represents single clones of each, so that the observations made at different places relate to genetically identical plants. *Freycinetia funicularis* is comparatively widely distributed in German botanic gardens, but its origin cannot be ascertained; however, it is a native of Indonesia, and probably was introduced from the Botanic Gardens in Bogor (formerly Buitenzorg), where it has been in cultivation for perhaps a century and still is common.

Freycinetia cumingiana (*F. luzonensis*) is a

Philippine species which came to Hamburg from the Bonn Botanic Garden, and according to the curator there, Dr. K. Kramer (pers. comm.), it was introduced to Europe via Tübingen from a source in the U.S.A., initially under the name "*F. cunninghamiana*." It has been possible to trace this clone back to its original source. Apparently it had been sent by E. D. Merrill from the Philippines to the New York Botanical Garden, from there to Puerto Rico, and to the Fairchild Tropical Garden in Miami, Florida, where it caught the attention of Dr. R. A. Howard of Harvard University, who reported his observations to Dr. B. C. Stone (see Table 1). Eventually this species found its way to Europe, perhaps from the Fairchild Tropical Garden.

OBSERVATIONS ON GROWTH AND SEX EXPRESSION

Observations on both species are summarized in Table 1. It is remarkable that despite the pronounced differences in shoot architecture (see Fig. 1), the two species have produced staminate and pistillate inflorescences, both sequentially and simultaneously. *Freycinetia cumingiana* apparently produces different kinds of shoots, predetermined to form either staminate or pistillate inflorescences. The latter are stouter and less ramified (Fig. 3). However, as shoot diameter decreases with age, the initially pistillate shoots convert to the production of staminate inflorescences. Evidently, shoot diameter and sex expression are correlated in this species. The qualitative "jump" may occur when the shoot diameter decreases to less than 4 mm (Fig. 2; Table 2). Perhaps this is also the diameter range wherein mixed inflorescences may form. In *Frey-*

¹ My thanks to Dr. B. C. Stone for encouragement, to Dr. K. Kramer for details on *Freycinetia cumingiana*, J. Bogner on *F. funicularis*, Dr. M. Fallen and Prof. Dr. K. Kubitzki for advice, and Mrs. H. Schwob-Tonn and our greenhouse staff for expert cultivation.

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TABLE 1. Comparison of growth and flowering of two species of *Freycesetia* in the Hamburg Botanic Gardens, 1982–1986.

	<i>Freycesetia funicularis</i>	<i>Freycesetia cumingiana</i>
Morphology	Large climber (“rooter”) with horizontal clinging roots and vertical roots; inflorescences lateral on at least one-year-old, still leafy shoots, often penetrating the leaf-bases.	Rhizomatous “leaner” with perennial shoots which may flower in 2nd year; inflorescences terminal on main axis or on rather elongated lateral shoots; shoots dimorphic, diam. ca. 5–6 mm in staminate shoots and 15–18 mm in pistillate shoots.
Flowering particulars		
1982	Abundant (ca. 50) inflorescences.	Several vegetative shoots; one fertile, with about 12 pistillate inflorescences.
1983	Abundant but exclusively pistillate inflorescences.	Only staminate inflorescences observed.
1984	Numerous staminate inflorescences plus a single pistillate inflorescence at the base of the plant; viable seeds and offspring obtained after hand-pollination.	Not recorded; allegedly staminate, but presence (or not) of pistillate inflorescences uncertain.
1985	Twelve staminate inflorescences, most produced later than usual after severe pruning had reduced the shade made by the plant itself.	Two ramified shoots with staminate inflorescences which had probably flowered the year before; 3 pistillate shoots, at least 2 flowering for the first time (Fig. 1); several fruits formed (no viable seed).
1986	No inflorescences on the old plant. Young plant (4 yr. old) with 12 staminate inflorescences mostly on vertical axes, 5 pistillate inflorescences on subapical parts of horizontally trained shoots, and one mixed inflorescence on a vertical shoot. Pollination yields fruits.	Staminate shoots continue to form staminate inflorescences; a pistillate shoot begins to produce staminate inflorescence on the distal parts (Fig. 2). Since 1984, only stout, apparently pistillate-determined shoots have been formed. New shoot formed in 1985 (diam. 6.2 mm) is pistillate.
Additional observations	Similar observations by J. Bogner in Munich Bot. Gard. Younger plants from cuttings first produced pistillate then both pistillate and staminate inflorescences in the next and subsequent years. Encke’s account (1958) of “ <i>Freycesetia insignis</i> ” probably refers to <i>F. funicularis</i> .	A somewhat different sequence of flowering has been observed by Dr. K. Kramer (Bonn Bot. Gard.): the first inflorescences were staminate; later, also pistillate inflorescences were produced on basal parts of the branches. Eventually also mixed inflorescences were observed. Attempts to pollinate were not successful; no karyogamy had occurred. Same sequence observed by Dr. R. A. Howard, noted in a letter to Dr. B. C. Stone: “Sexes are a problem. I recall seeing pollen from one ‘flower’ but all I have are pistillate” (March 1969). “I assume the plant reproduced vegetatively and was completely female until this February, when I found an inflorescence producing pollen” (April 1969).

cinetia funicularis, this shoot differentiation is lacking, so that the synchronized formation of exclusively pistillate inflorescences in 1983 is unexplained. However, it seems to indicate that an adjustment over the whole vegetative body can take place, which may be hormonally (or

nutritionally) determined. Observations made in the Munich Botanical Garden by Josef Bogner (pers. comm.) suggest that larger and vigorous plants of *F. funicularis* may develop inflorescences of both sexes.

It is difficult to assign these *Freycesetia* species

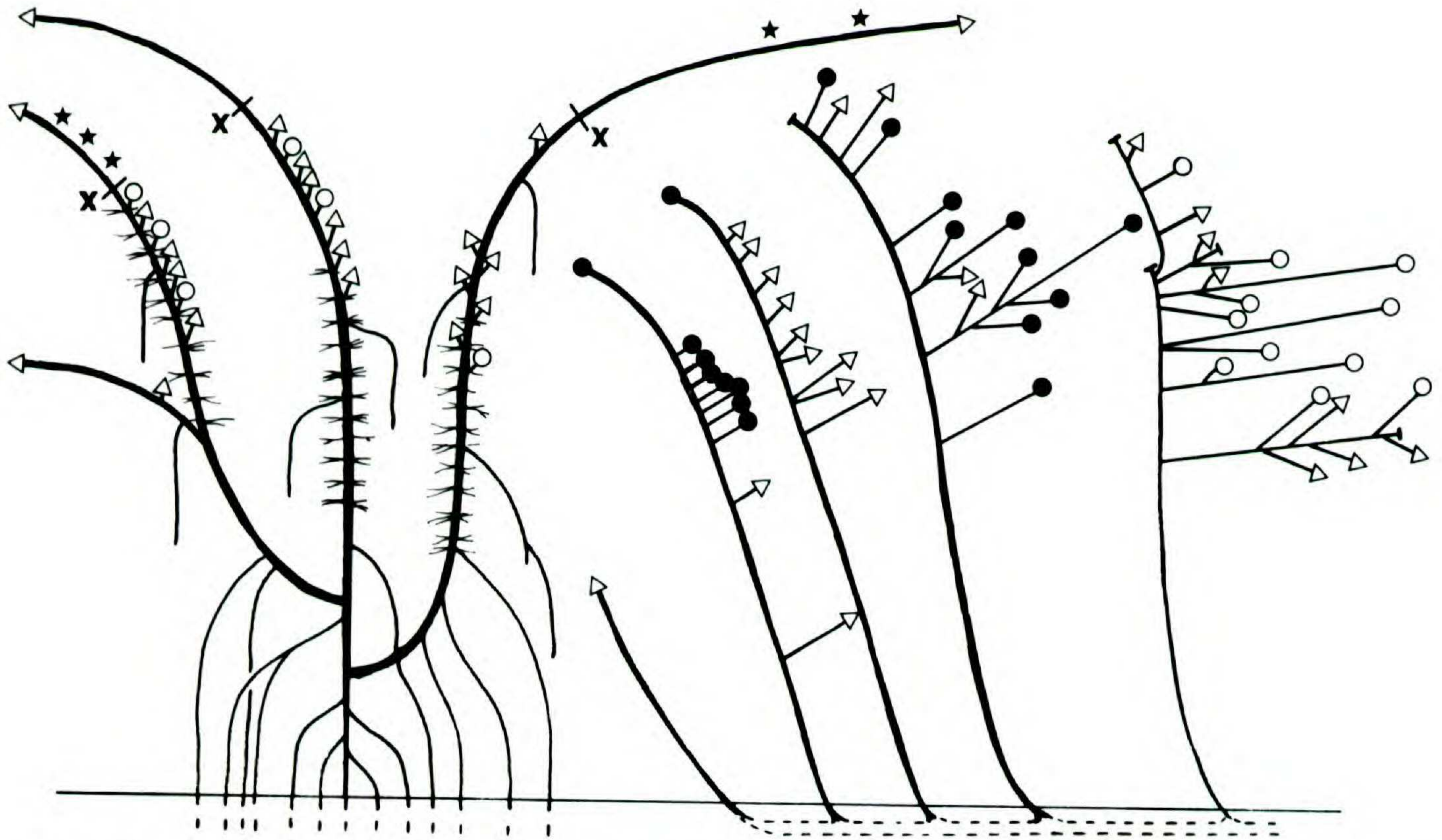


FIGURE 1. Diagrammatic sketch of shoot architecture in two species of *Freycinetia*. Pistillate inflorescences—black circles; staminate inflorescences—open circles; vegetative shoots—open arrows. Left: *Freycinetia funicularis*, an approximately three-year-old plant raised from a cutting, flowering for the first time; inflorescences, adventitious shoots, and clinging roots formed on at least one-year-old parts of the main shoots. X—plant trained horizontally from this point. ★—pistillate inflorescences formed here in the year to come. Right: *Freycinetia cumingiana*, showing (left to right) shoot of present year, two pistillate shoots formed during previous year, flowering for the first time, a two-year-old pistillate shoot, and a (probably) three-year-old staminate shoot. Note acrotonous ramifications, and “opportunistic” distribution of inflorescences and vegetative shoots probably influenced by different degrees of shading.

to one of the architectural models of Hallé et al., although some species have been so assigned by Castro dos Santos (1981). This is because the “opportunistic” growth of these lianas with easily formed accessory shoots makes it difficult to distinguish between homogeneous vs. heterogeneous axes and orthotropic vs. plagiotropic growth. In *F. cumingiana*, inflorescences are always terminal on the main shoot as well as on the lateral shoots, so that branching in the floral region is monopodial, except for occasional vegetative shoots. In *F. funicularis*, the inflorescences are lateral on short shoots.

When the staminate and pistillate inflorescences were produced simultaneously, hand-pollination of the latter resulted in fruit formation; in *F. funicularis* seeds from such fruits germinated to produce viable seedlings. In *F. cumingiana*, attempts to pollinate by hand were unsuccessful in both Hamburg and Bonn Botanic Gardens. Although the pistillate heads enlarged considerably and were not aborted, fertilization apparently did not occur; at least the pollen was

able to trigger development. It may be noted that in the related genus *Pandanus*, no pollen stimulus is necessary, at least in some species, and parthenocarpy is normal. It must be remembered that attempts to pollinate tropical plants in temperate-zone greenhouses are chancy, for even if the basic aspects of the breeding system and the receptive period of the stigmas are understood, it may be impossible to obtain fertilization. An example of this difficulty is *Cinnamomum verum* (*C. zeylanicum*), the true cinnamon, as recounted by Kurz (pers. comm.). On the other hand, if pollination is successful, the possibility of pseudogamous agamospermy cannot be ruled out (Gadella, 1983). These observations are casual but may serve as the basis for some speculations, if only for the purpose of stimulating further experiments (which cannot be performed with scarce material in cultivation).

The evolutionary significance of dioecy has received recent attention, as in a symposium volume (Ann. Missouri Bot. Gard. 71: 243–296, 1984) where a survey of the subject and further

TABLE 2. Branch diameter and sex expression in *Freycinetia cumingiana*.

The axis was measured ca. 3 cm below the inflorescence (to avoid the expansion immediately below it). The pistillate shoot measure is that shown in Figure 2. The respective means are $m_a = 3.98 \pm 0.38$ mm for pistillate inflorescences, $m_b = 3.08 \pm 0.35$ mm for staminate inflorescences on pistillate shoots, and $m_c = 2.76 \pm 0.26$ mm for staminate inflorescences on staminate shoots. Branch diameter for pistillate inflorescences differs significantly from that for staminate inflorescences.

Branch Diam. (in mm)	Pistillate Inflores- cences	Staminate Inflorescences	
		♀ Shoots	♂ Shoots
1.6–2.0			1
2.1–2.5		1	4
2.6–3.0	1	4	11
3.1–3.5	2	2	3
3.6–4.0	12	2	
4.1–4.5	5		1
4.6–5.0	4		

references may be found. Discussion centers around the question of whether the so-called benefits of dioecy (Willson, 1983) are genetically or ecologically determined, i.e., whether the promotion of outcrossing or ecological constraints on reproduction are evolutionarily decisive. This matter need not be resolved here, but our concern is with occasional departures from dioecy, a phenomenon that has been termed “leaky dioecy” by Baker & Cox (1984). Such leaky dioecy may be considered as one prerequisite for successful colonization of remote islands, since propagation by selfing becomes possible. Apomixis is another kind of solution to this problem, as is the parthenogenesis observed in some insular animal populations (e.g., Cox in White, 1985; Mau, 1978).

Rohwer & Kubitzki (1984) recently reported an interesting example of leaky dioecy in the neotropical riverine willow *Salix martiana* Leyb., which was found to produce regularly mixed catkins with staminate, pistillate, and perfect flowers. This was attributed to the difficulty of producing offspring after a probable long-distance dispersal and in an unstable environment. Mixed catkins are not uncommon in *Salix* (Velenowsky, 1904; Toepffer, 1925) but the high incidence in a tropical species, certainly much less studied than its temperate congeners, suggests that here

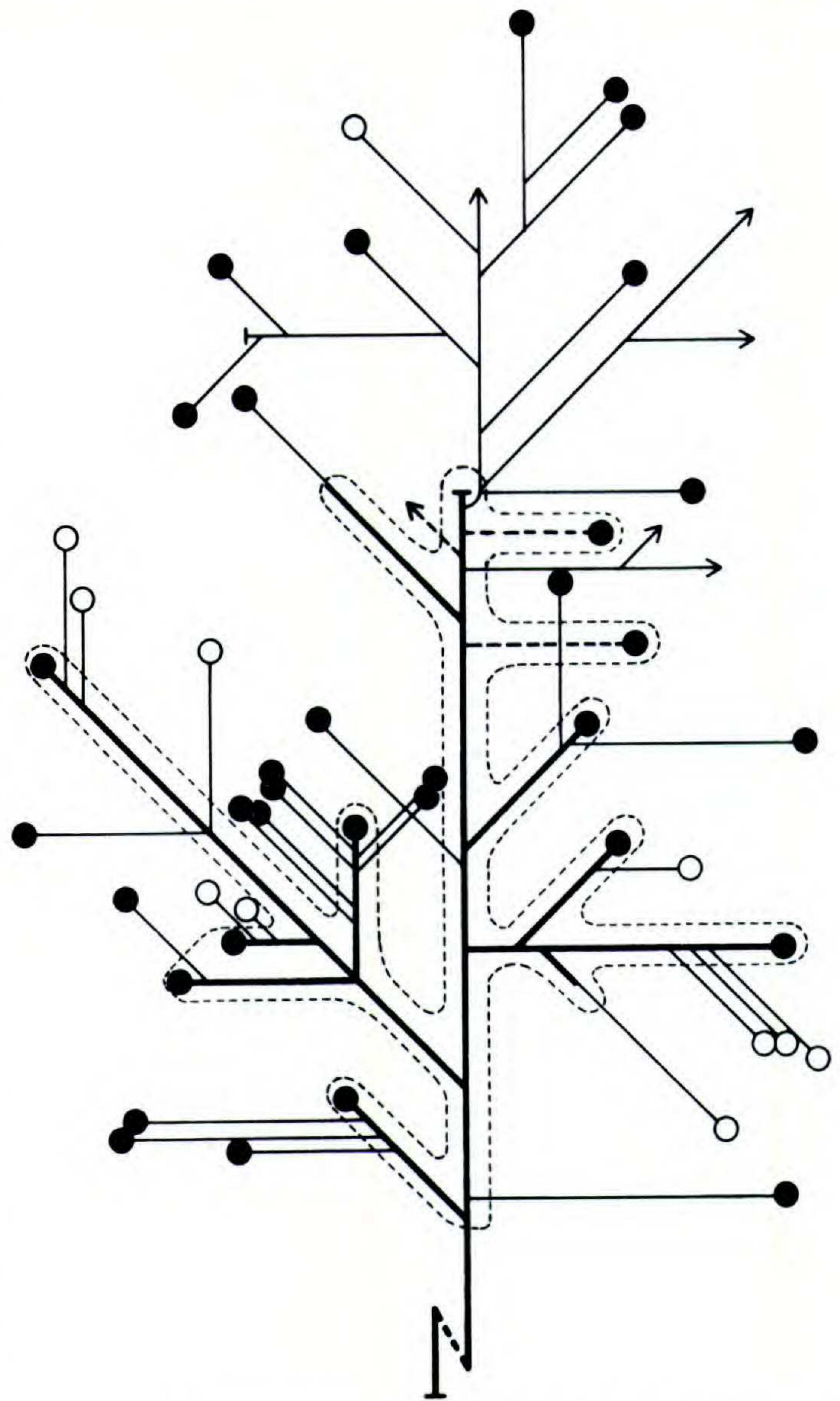


FIGURE 2. Diagrammatic sketch of sex expression on an initially pistillate shoot in two successive years. The broken line marks the state in spring, 1985; compare with the shoot second from left in Figure 1, but note that due to the straggling habit and the necessity of training the climber, some shoots may have been removed. Note further that the staminate inflorescences (open circles) formed on the distal parts of the shoot in 1986.

it is a more or less regular phenomenon. Although hermaphroditic flowers are unknown in *Freycinetia*, the two genera may be taken as parallel cases for the evolution of monoecy (which may be a reversal of a previous evolutionary trend from monoecy to dioecy). Another aspect of this possible parallelism will be discussed next.

Developmental plasticity is one of the characteristics of liana species, as exemplified by their “opportunistic” shoot architecture in comparison with trees (Etifier, 1981). This plasticity is needed to adjust to a temporarily very heterogeneous habitat, where, for instance, light intensity encountered by juvenile plants is drastically different than that encountered by adults. In

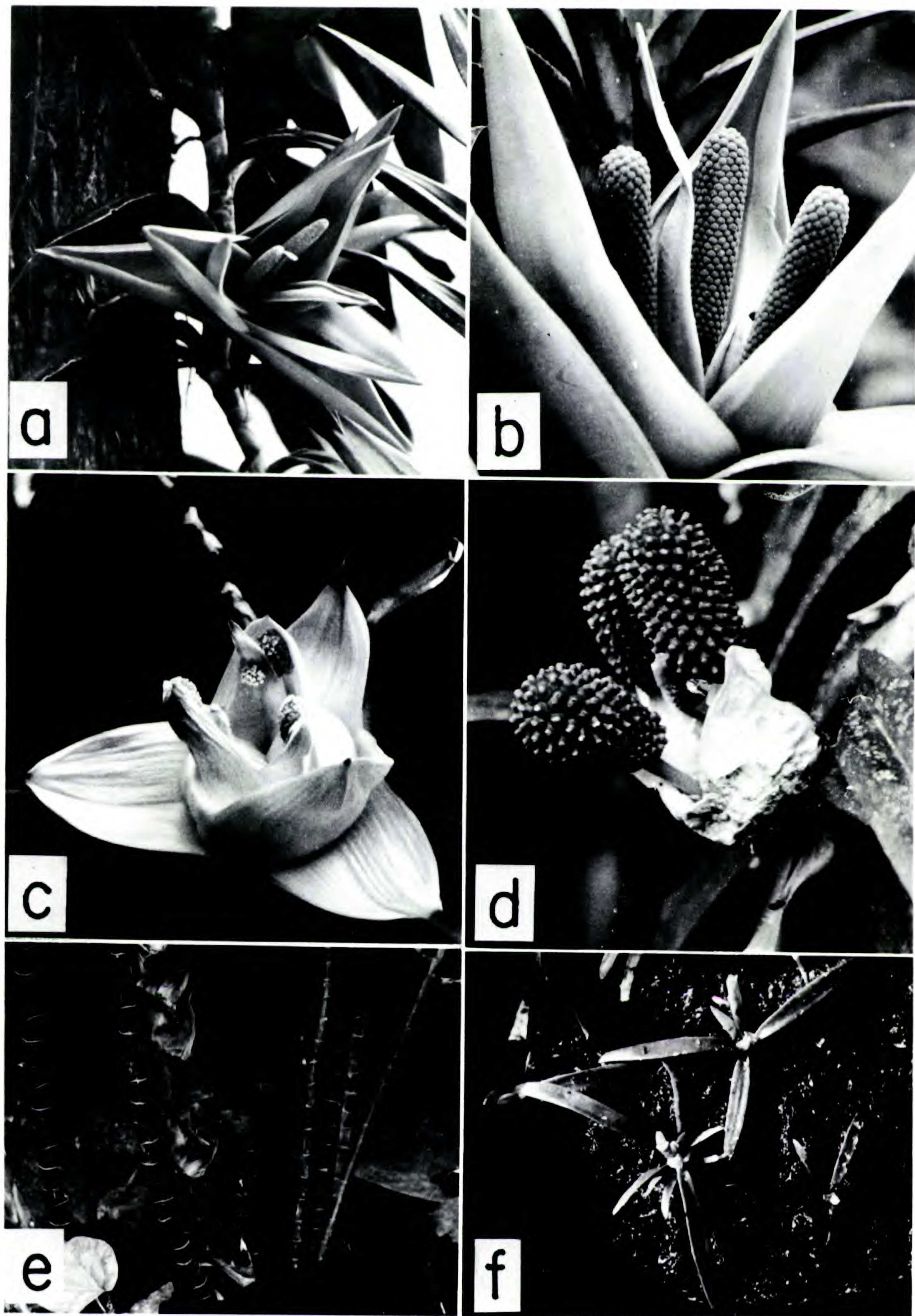


FIGURE 3. Aspects of growth of two *Freycinetia* species. a, b. *Freycinetia funicularis*.—a. Staminate inflorescence on a vertical shoot, ca. 18 cm diam.—b. Pistillate inflorescence at anthesis (spikes 8 cm long). c–e.

Freycinetia, at least in the two species observed for this study, such plasticity extends to sex expression. This is not surprising since environmentally determined sex expression has several selective advantages for species living in a "patchy" environment (Charnov & Bull, 1977; Willson, 1983), and sequential hermaphroditism has been reported for many species. The factors invoked include light intensity (e.g., *Catasetum*; Dodson, 1962), hormonal and nutritional status (e.g., *Elaeis guineensis*; Williams & Thomas, 1970), or disturbance of vegetative parts (e.g., *Arisaema*; Schaffner, 1921), all of which may interact variously, and all of which may be applicable to the present cases. Thus, in *F. funicularis*, horizontal training of the branches may have altered the hormonal balance toward the production of pistillate inflorescences; exhaustion of nutrient reserves, self-shading of shoots, or pruning may have been responsible for the switch back to staminate inflorescence production. Experimental proof for this would be difficult to obtain. At least, the size-correlated sex expression in plants of *F. cumingiana* will permit further study. Cuttings have been made from the differently determined axes and their fate will be observed in coming years.

Clearly it should not be too difficult to find plausible explanations for the adaptive values of dioecy, monoecy, or plasticity in sex expression in a given situation. However, the phenomenon of leaky dioecy is still puzzling. Why is it restricted to certain genera and absent in others? Why, for instance, are no such cases known in *Populus* or in *Pandanus*, which are the sister genera of *Salix* and *Freycinetia*, respectively? In *Populus* and *Pandanus* pollination is believed to be chiefly by wind (Toepffer, 1925; Cox, 1982). A possible explanation is that in anemophilous plants, the staminate and pistillate functions must suit quite different needs and, as a result, tend to evolve divergently. Such divergence seems improbable in zoophilous groups, where a high degree of similarity is advantageous (in overall form, size, color, odor, and perianth details, though not in the details of staminal and gynoecial form). The correlation of leaky dioecy with

change from anemophily to zoophily is a possibility worth investigating.

To obtain evidence bearing on these questions, many more observations are needed, preferably on the same specimens over a number of years. The statement by Cox et al. (1984) about the value of living collections for this kind of study may be emphasized again. Phenomena such as these tend to escape the notice of both purely field- and herbarium-oriented workers, but botanic gardens provide an excellent location in which to study such things as "leaky dioecy."

VOUCHER MATERIALS

Herbarium material of both *Freycinetia* species discussed is deposited in PH and HBG, and the behavior of *F. funicularis* is also documented in M (*Bogner 1783*). Additional prints for photographic documentation are on deposit in PH and HBG.

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Freycinetia cumingiana. —c. Staminate inflorescence ca. 6 cm diam. —d. Pistillate inflorescence after anthesis, spikes 1.5–2 cm long. —e. Basal parts of shoots (from left to right, two old pistillate shoots, current pistillate shoot with caducous bracts, three pistillate shoots interspaced with two staminate shoots, the latter much thinner). —f. *F. funicularis* seedlings ca. six months old, their leaves about 2 cm long.

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